The Role of Carnivores in Conservation

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Final Report

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The role of carnivores in conservation

A major theme in vertebrate ecology in the last decade of the twentieth century has been the contribution of carnivores to the function of communities and ecosystems, and the importance of these and carnivores in general to issues of biodiversity conservation. The kinds and importance of interactions between carnivores and other ecosystem components are discussed often (Estes 1995, Terborgh et al. 1999). Carnivores are now believed to affect community structure and ecosystem processes in ways that would have evoked skepticism 20 years ago. Often described as top-down effects or trophic-cascades, some of these carnivore-mediated processes serve to maintain native biodiversity; others tend to erode it.

Functions of carnivores in communities and ecosystems

Traditionally, carnivores were seen as potentially, but not necessarily affecting density and demography of prey. Considerable literature (e.g. Caughley et al. 1980) has addressed whether and how carnivores control or regulate prey populations by killing or causing fitness-reducing behaviors (Lima 1998). Often, however, the search for predator effects on prey has yielded inconclusive and context-specific answers, resulting from the high reproductive rates of some prey species, the compensatory nature of predation and other mortality causes (Errington 1946), and complex trophic interactions where carnivores switch prey or prey have multiple predators (Boyce and Anderson 1999).

In recent years, however, ecologists have demonstrated or proposed roles for predators, particularly the Carnivora, that are diverse, cross multiple trophic-level boundaries, that shape communities and entire ecosystems. These include trophic

cascades that extend to primary producers (Schmitz et al. 2000), nutrient transport and plant fertilization by aquatic predators that defecate on land (Ben-David et al. 1998) and dispersal of seeds and spores (Willson 1993), in some cases of plants important in successional sequences (Hickey et al. 1999). Of course, carnivores have always been recognized as completing or interrupting the life cycles of parasites, although which of these roles is most important is unclear (Price 1990).

These reported effects of carnivores have qualified some to be keystones, species that make disproportionately large contributions to community function (Power et al. 1996). Sea otters (*Enhydra lutr*is) exert top-down effects on invertebrates and macroalgae (Power et al. 1996), wolves (*Canis lupus*) have been alleged to regulate woody vegetation via effects on herbivores (Post et al. 1999), and introduced arctic foxes (*Alopex lagopus*) dominate the avifauna of some Aleutian Islands (Bailey 1993). Berger et al. (in press) concluded that the elimination of wolves and brown bears from Grand Teton National Park, Wyoming, along with the prohibition of moose hunting there, has reduced vegetation structure at browsing heights. This, in turn, has reduced abundance and richness of shrub-nesting riparian birds inside the park compared with outside, where human hunting had substituted for predation by large carnivores. Thus, a carnivore-dominated, top-down, bottom-up mechanism controls neotropical migrant birds.

It is, if anything, surprising that carnivores are not even better represented among keystones, given that high trophic level predisposes species to keystone status (Paine 1995). Allometric equations predict that carnivore populations will be only 8-56% as dense as those of mammalian herbivores of the same body size, and about 3% as dense as their typical mammalian prey, which tend to be an order of magnitude smaller than

themselves (Peters and Raelson 1984). Thus, any contributions that carnivores may make to community function would tend to outweigh their numerical or biomass representation, yet only one marine and one terrestrial taxon out of over 30 known or likely keystones in those two biomes tabulated by Power et al. (1993) were carnivores. One reason that researchers heretofore may have tended to overlook the functions of carnivores is that the spatial scale of studies has not matched that of the effects; recent emphasis on landscape-scale phenomena may have improved our understanding of wide-ranging species like carnivores.

Another, increasingly recognized role of carnivores is that of structuring non-prey species through interspecific competition, of which two kinds have been described. Exploitation competition occurs when one animal consumes a limiting resource before its competitor, whereas interference competition occurs when an animal acts aggressively toward one of a different species (Keddy 1989). Exploitation competition among carnivores has not been demonstrated, but interference is documented often, and commonly leads to reduction or local extinction of the subordinate species (Buskirk 1999), with major implications for community structure. Wolves on Isle Royale in Lake Superior and on the Kenai Peninsula of Alaska have been credited with eradicating coyotes upon their arrival in the former place (Krefting 1969), and with preventing the sympatry of coyotes before the extinction of wolves in the latter (Thurber et al. 1992). Many, if not most mammalian carnivores in North America have been implicated in these interference competitive interactions (Buskirk 1999, Table 7.2; Fig. 1), which tend to be strongly size-mediated. Winners tend strongly to be are larger-bodied, and the strongest interactions tend to occur between species that are similar in body size and shape

(Buskirk 1999, Buskirk et al. 2000). Thus, bears (~10^2 kg body weight) compete little with weasels (*Mustela* sp.; ~10^{-2} kg body weight), but brown bears (*Ursus arctos*) can compete fiercely with black bears (*U. americanus*) (Mattson et al. 1992). The median difference in body weights between participants in interference competitive interactions shown in Fig. 1 is a factor of 3; interference is uncommon between carnivores that differ in size by a factor of more than 8.

Carnivores and conservation

Among the generally strong ecological effects of carnivores are those related, positively and negatively, to the conservation of native vertebrates. Carnivores are themselves species of conservation concern, accounting for a high proportion of sensitive, threatened, and endangered taxa. Carnivores constitute 22% of mammalian species listed under the Endangered Species Act (http://ecos.fws.gov/tess/html), but only about 12% of mammal species in the U.S. (Jones et al. 1997). Similarly, Newmark (1995) found that mammalian species that had become extinct in national parks of western North America after the establishment of those parks were strongly skewed toward carnivores (22 of 29 extinctions). Mid-sized carnivores (1 - 15 kg body weight) accounted for only 21% of the species Newmark studied, but over half of the extinctions observed. This is explained simply by the low population densities of carnivores and stochastic and genetic processes found in small populations.

The coyote, a keystone in the right context

In contrast, carnivores also are the proximal causes of the loss of native biodiversity by reducing a wide range of sensitive, threatened. or endangered species (Reynolds and Tapper 1996, Witmer et al. 1996) through predation and competition. Perhaps no native North American vertebrate exerts more powerful and widespread, yet more context-dependent effects on the conservation of native vertebrates than the coyote (Table 1, Fig. 2). This influence reflects the coyote's consummate adaptive ability: its body size evolves quickly (Thurber and Peterson 1991), and its diet can include fruits, native birds and mammals (Bekoff 1982), allochthonous marine invertebrates (Rose and Polis 1998) and domestic pets. Its social organization varies with prey type, its reproductive output tracks resource conditions, and it succeeds in wilderness and urban settings. Coyotes hybridize readily with other sympatric *Canis*, so that their genes are carried by wolf-like (Roy et al. 1994) and dog-like strains, some highly successful. And, they are expanding their geographic range: formerly uncommon in many areas that were forested or dominated by wolves, coyotes have increased in Alaska and Minnesota in the last 100 years (Manville and Young 1965); in forested areas of the northwestern U.S., the northeastern U.S. and eastern Canada in the last 30 years (Buskirk et al. 2000); and in southern Florida in the last 20 years (Maehr 1997).

Coyotes have been implicated in limitations and declines of many birds and mammals of conservation concern (Table 1), in some cases inflicting most known-cause mortality or killing >50% of the population yearly. They have killed 24-63% of populations (50-87% of all deaths) of the endangered San Joaquin kit fox (White and Garrott 1997), and caused 63% of all deaths of the kit fox in Kansas. Similarly, the coyote was the primary predator of eggs and caused 39% of the deaths of young whooping cranes, also

endangered (Drewien et al. 1985), and caused 56-66% of all deaths, and 76-91% of predation deaths of the endangered Columbian white-tailed deer (U.S. Fish and Wildlife Service 1998). Of course, coyotes are the primary predators of many native species that are not conservation concerns, for example causing 41-50% of deaths of cottontail rabbits and snowshoe hares (Cox et al. 1997), and removing >37% of neonatal white-tailed deer recruitment within 21 days of birth (Knowlton and Stoddart 1992).

Coyotes also, in suitable contexts, compete with species that depredate species of conservation concern, thereby sustaining native biodiversity. In arroyo chaparral communities of southern California, where wolves (*Canis lupus*) were absent from the pre-settlement guild, the loss of coyotes via habitat fragmentation has caused smaller carnivores (feral cats [*Felis catus*], gray foxes [*Urocyon cinereoargenteus*]) to increase (Crooks and Soulé 1999), causing a decline, in turn, of passerine birds that nest near the ground (Fig. 2). Coyote control in the northern prairie of the U.S. has led to reduced abundance of red foxes, but not of other mesopredators, and increased survival of duck nestlings (by a factor of 1.9), which was explained by lower predation on nestlings inflicted by coyotes than by foxes (Sovada et al. 1995). This "mesopredator release" hypothesis has been applied widely in recent years to explain how body-size-structured carnivore communities, typically including the coyote (Fig. 2), can affect the abundance and diversity of prey down to the size of wrens. Mesopredator release assumes two properties of carnivore - prey communities: first, optimal prey size is positively related to carnivore size: predators (except for filter feeders) do not prey on animals much smaller than themselves. Second, carnivores are most intolerant of allospecifics that are similar in size to, but smaller than themselves. Both of these are generally supported (e.g.

Rosenzweig 1966 for prey size), but the exact mechanisms underlying mesopredator release are often undemonstrated and assumed. Table 1, shows how the loss of coyotes is variously crediting with increasing small mammals (Henke and Bryant 1999) and reducing small birds (Crooks and Soulé 1999) through similar mechanisms.

Yet, coyotes can be reduced to relative ecological impotence by the addition of a morphologically similar, larger carnivore, the wolf. Coyotes have declined in density or disappeared completely in most places where the wolf has recolonized or been reintroduced. Therefore, the obvious solution to the negative conservation effects of the coyote is to restore the wolf to its pre-settlement ecological role: predator of ungulates, and top canid competitor. How plausible is this? The recent downgrading of the wolf from endangered to threatened in the contiguous United States reduces the likelihood that coyotes will be returned to their presettlement ecological distribution and role. So, we must learn to coexist with coyotes, or reconsider our policies for reintroducing wolves on the basis of their ecosystem contributions, rather than on the basis of their conservation status.

Is the coyote the nemesis of terrestrial biodiversity or the savior of terrestrial bird and mammal biodiversity in top-down trophic and competitive systems? The answer is either and both: it depends on the body size of the species of concern. For species somewhat smaller than coyotes (ca. 1/3 - 1/10 the size), coyotes clearly have strong negative effects, whereas for much smaller species (<500 g), the effects of coyotes tend, with exceptions, to be positive (Table 1), because of predation on and competition with mammals intermediate in size between coyotes and these smallest birds and mammals. The same

body-size structuring of communities should be found, in principle, in all carnivores. However, the coyote is unique in occupying a mid-point in the size range of North American mammalian carnivores, and in its extraordinary ecological and evolutionary adaptability.

The new findings that attribute to mammalian carnivores previously unrecognized importance in the structure and function of terrestrial communities and ecosystems have important implications for conservation of natural systems and native vertebrates. Carnivores are being shown to affect a wide range of species at various trophic levels and via direct (predation and interference competition) and indirect modes of action. Of these, the direct effects on prey or subordinate competitors are best-documented. Other effects across two or more trophic levels are less clear, but if corroborated by future research, would transform our understanding of the driving forces in terrestrial bird and mammal communities. However, the roles (sustaining or eroding biodiversity) depend on the body-size relationships of the species participants, and in some cases lack explanatory mechanisms.

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Figure captions

Figure 1. Interference competitive interactions reported for North American carnivores. Arrows, pointing from dominant toward subordinate participants, in all cases show larger species dominating smaller ones, with few interactions between pairs of species that differ in size by a factor of >8. Modified from Buskirk et al. (2000).

Figure 2. Reported mesopredator release effects involving the coyote and smaller-bodied species, showing the body-size relationships of the participants. All arrows show the effects of loss or removal of coyotes. Sideways arrows indicate no effect found.

but may themselves be affected by even larger carnivores (Estes et al. 1998)